

## RESISTANCE TO PULL-OUT OF CHILEAN RIVERINE SPECIES: EVIDENCE FROM LABORATORY EXPERIMENTS

G. Piqué<sup>\*a,b</sup>, L. Mao<sup>b,c</sup>, P. Becerra<sup>b</sup>

<sup>a</sup> Escuela de Agronomía, Facultad de Ciencias Agronómicas y de los Alimentos, Pontificia Universidad Católica de Valparaíso, Quillota, Chile<sup>1</sup>

Departamento de Ecosistemas y Medio Ambiente, Facultad de Agronomía e Ingeniería Forestal, Pontificia  
Universidad Católica de Chile, Santiago, Chile

<sup>c</sup> School of Geography, University of Lincoln, Lincoln, UK

<sup>1</sup>Present address for the corresponding author G. Piqué has changed from ‘Pontificia Universidad Católica de Chile’ to ‘Pontificia Universidad Católica de Valparaíso’. Current e-mail: [gemma.pique@pucv.cl](mailto:gemma.pique@pucv.cl)

## 23    **ABSTRACT**

24    Vegetation growing in river bars and banks determines the morphological processes in river  
25    channels. The presence and dynamics of riverine vegetation depend on the magnitude and  
26    frequency of floods able to change morphology and uproot plants, and on the plant's resistance to  
27    pull-out. A series of pull-out experiments were carried out with the objective to determine the  
28    resistance of riverine vegetation to be uprooted and its effects on river-bed dynamics. Nine riverine  
29    species were used for the experiment: seven of them are native from Chile, and the other two are  
30    exotic and invasive in Chilean environments. A total of 200 specimens were transplanted in a  
31    substrate simulating a bar of a gravel-bed river, and after 7 months they were individually pulled-  
32    out, and the force and time needed to uproot the plant quantified. Data were analysed by means of  
33    generalised linear models (GLM) and linear regressions, and force-time curves were interpreted and  
34    related to the root morphology of the species. GLM results showed that resistance values are  
35    dependent on root and plant physical characteristics, and by the factor species. Among the species  
36    studied, the three species showing higher resistance values were native, while the less resistant was  
37    an exotic invasive species. The time needed to uproot the individuals did not seem to be influenced  
38    by plant parameters nor by the factor species. Root architecture seemed to have an effect on plant  
39    pull-out resistance and uprooting rapidity, being heart-shaped roots the ones that registered higher  
40    resistance values. Despite this, when incorporating flow strength on the findings, the exotic invasive  
41    ones seemed to be some of the more resistant to uprooting. The findings of this paper contribute to  
42    the better understanding of river vegetational and sedimentary dynamics, and are useful for  
43    parameterising the modelling of fluvial landscapes evolution and for the design of river restoration  
44    projects.

45    Keywords: pull-out resistance; vegetation uprooting; gravel-bed river; central Chile

## 46 1. INTRODUCTION

47 Riparian vegetation exerts a great influence on river channel morphology by stabilising and  
48 trapping sediments, and originating abundant and diverse fluvial forms (Gurnell, 2014). During  
49 flood events, vegetation may be removed from bars, margins, and floodplains, thus vegetation  
50 dynamics depend on the occurrence and magnitude of these disturbances (Gurnell et al., 2012). The  
51 complex interaction between flow and vegetation has been assessed in several studies. For instance,  
52 Bankhead et al. (2017) described both the driving and resistance forces acting on riverine vegetation  
53 when immersed. They identified water flow as the driving force acting on vegetation, and  
54 vegetation root anchoring as the main resisting force to uprooting. The complex series of feedbacks  
55 and interactions between vegetation and fluvial landforms processes was conceptualized in terms of  
56 “fluvial biogeomorphic succession” (Corenblit et al., 2007). This bi-directional interaction occurs at  
57 all stages of vegetation growth, but young seedlings are more susceptible to be detached by high  
58 flow pulses and floods, while mature individuals are more capable of recovering after partial  
59 uprootings due to floods (Crouzy, 2014). This generates a selective removal of the weaker  
60 vegetation on bars and margins (Perona et al., 2012; Crouzy et al., 2013).

61 Edmaier et al. (2011) classified the mechanisms of plant uprooting in two types: I) uprooting of the  
62 whole plant due to flow drag forces, and II) uprooting due to local sediment erosion around the  
63 plant, which exposes the roots and reduces root anchoring. According to these authors, type I  
64 detachment mechanism occurs in a very short time, and depends on root amount and characteristics  
65 (e.g. diameter, length, strength). Type II detachments occur more gradually, since root-anchoring  
66 forces are progressively reduced due to the higher exposure of roots after an erosion period. The  
67 resistance of riparian vegetation to pull-out has been quantified both in the field (e.g. Karrenberg et  
68 al., 2003; Abernethy and Rutherford, 2001), and in laboratory conditions (e.g. Xavier et al., 2010;  
69 Edmaier et al., 2015). Giadrossich et al. (2017) described the variety of experimental methods that  
70 have been used to measure root strength in hillslopes. Among them, three instruments were found to  
71 be applied in riverine environments: i) root-pullers to remove the entire plant from the substrate  
72 (e.g. Karrenberg et al., 2003; Bankhead et al., 2017); ii) root-pullers to pull up individual roots from

the substrate (e.g. Abernethy and Rutherford, 2001; Bankhead et al., 2017); and iii) tensile testing machines to stretch individual root segments extracted from soil until their failure (e.g. Edmaier et al., 2014; Capilleri et al., 2016). The three approaches use apparatus based on similar technology: i.e. plants or roots attached to a load cell or a transducer and to a puller device at the other end. Numerous experiments showed that the pull-out resistance of plants and roots in stream banks is influenced by specific specimen characteristics: e.g. stem or root diameter (Bankhead et al., 2017; Osman et al., 2011; Calvani et al., 2019), number of roots (Edmaier et al., 2011), or root length (Bywater-Reyes et al., 2015). However, few focused on the time required to uproot a specimen. Besides plant characteristics, sediment material and substrate moisture also affect plant resistance to pull-out (Pollen, 2007). In this sense, less sediment moisture content implies greater force to uproot plants (Edmaier et al., 2014); and in riverine non-cohesive environments, higher pull-out resistances are observed in sand river-beds compared to gravel-beds (Karrenberg et al., 2003).

River channels are specially fragile and susceptible to vegetation invasions (Hood and Naiman, 2000; Castro-Díez and Alonso, 2017). The high presence and spread of exotic species in fluvial corridors are frequent in anthropogenic disturbed rivers (Richardson et al., 2007; Arianoutsou et al., 2010). At the same time, rivers constitute an easy way for seeds and propagules to spread by water (Pyšek and Prach, 1994; Richardson et al., 2007). Moreover, floods can contribute to a higher spreading of the seeds of invasive species by increasing the availability of nutrients and by the disturbances of native vegetation (Čuda et al., 2017). Among the wide range of invasive species, Australian *Acacias* are known to be invasive worldwide (Le Maitre et al., 2011) and, in particular, *Acacia dealbata* and *Acacia melanoxylon* are common in Chilean fluvial environments (Fuentes-Ramírez et al., 2010; Batalla et al., 2018). To the knowledge of the authors, it is unknown whether riverine exotic species differ from natives in the resistance to pull-out. Although riverine native species should have some resistance to uprooting by floods, a higher resistance to pull-out by riverine exotic species may explain their important abundance in fluvial habitats.

The main objective of this study is to determine the resistance of riverine vegetation to be uprooted and its effects on river-bed dynamics. Specific objectives of the paper are: i) to determine the

influence of root characteristics and root morphology on the species resistance to uprooting, ii) to study the effects of different hydrological conditions on the resistance to uprooting, and iii) to assess whether exotic invasive species are more resistant than native species. To respond to the objectives, the uprooting resistance of 9 species from Chilean riparian environments was measured in a series of plant pull-out experiments in controlled conditions. In order to reproduce similar conditions found in the field, the uprooting experiments reproduced the type I erosion defined by Edmaier et al. (2011) on young individuals growing on a non-cohesive substrate simulating a gravel-bed river.

## 2. EXPERIMENTAL DESIGN AND METHODS

### 2.1. Experimental design

An assortment of 200 individuals of 9 bushy and tree species commonly found in Chilean riparian environments were used in the experiment (Table S1 in Supplementary material). We selected species commonly growing in the Mediterranean region of Chile. Among them, 7 are native from Chile (i.e. *Aristotelia chilensis*, *Cryptocarya alba*, *Escallonia illinita*, *Fuchsia magellanica*, *Lithraea caustica*, *Maytenus boaria*, and *Quillaja saponaria*), and 2 are exotic (i.e. *Acacia dealbata* and *Acacia melanoxylon*). Both were introduced for ornamental purposes in the late 1800s (*A. dealbata*) and early 1900s (*A. melanoxylon*), and have a high invasive potential (Fuentes et al., 2014). Among native species, *Escallonia illinita* and *Fuchsia magellanica* grow exclusively in riparian habitats throughout the Mediterranean region of Chile, while the other species may also be found in other habitats of this region. Both exotic species also grow in riparian habitats in the Mediterranean region of Chile.

Plants were selected in order to be as much similar in terms of stem diameter and height between individuals of the same species at the beginning of the experiment. All specimens were 1 year old, except the *Acacia dealbata*, which germinated a year before. Specimens were growing on small cylindrical plastic bags (volume between 400 and 800 cm<sup>3</sup>).

In order to simulate the conditions of plants growing on alluvial bars of a common gravel-bed river, the specimens were transplanted on much larger plastic growing bags (diameter = 22.5 cm, height = 37 cm, volume ~ 14,700 cm<sup>3</sup>) filled with a substrate composed mainly of sand, gravels and cobbles ( $D_{50} = 15.67$  mm;  $D_{max}$  class = 31.5 mm; Fig. 1), thus replicating a non-cohesive environment.

Transplanted individuals were grown inside a nursery during almost 7 months (from 25-31 of July 2018 to 24-30 of January 2019, Fig. 2a and 2b) to allow for the roots to develop during most of an entire growing season. All plants were equally and regularly watered when needed, depending on the weather conditions and humidity of the substrate. The growth of all individuals was monitored monthly by measuring their stem diameter and height. Moreover, the root systems of one individual per species were scanned using WinRizho<sup>®</sup> software before transplanting and at the end of the experiment to have an approximation of root growing during the period by measuring the root length, root area, average root diameter, and root volume.

The plant pull-out experiments were performed between the 25<sup>th</sup> and 30<sup>th</sup> of January 2019. The pull-out mechanism (Fig. 2c, 2d and 2e; and Video 1 and 2 in Supplementary material) consisted on a load cell, connected to an electric winch located at the top of a tripod, and attached to the base of the stem of a specimen, by means of a carabiner and wrap tape. The load cell (PCE-FB 5K, PCE-Instruments<sup>®</sup>) measured at 0.1-second intervals the strength offered by the roots during the pull-out experiments, resembling to the previously done in similar experiments (Osman et al., 2011; Bankhead et al., 2017). Pull-outs were performed vertically and at the same distance in order to ensure the same treatment to all individuals, despite the effects of pull angle on the strength lecture are minimal (Gupta et al., 2008). The experiments allowed to obtain continuous curves of the strength needed to remove the plant over time. From this data, the maximum resistance of the individual ( $R_{max}$ ) and the time needed for removal ( $T_{to\_max}$ ) were calculated. Individuals were also measured both in their aerial part (stem diameter and height) and roots (diameter at 2 cm depth), and weighted and dried in the oven (45°C, 72 h) to obtain dry biomass.

## 2.2. Data analysis

### 2.2.1. Evaluation of plant resistance to pull-out.

Overall, successful pull-out runs were completed for 180 individuals. Four different plant parameters were selected as predictors or independent variables: root cross-sectional area at 2 cm depth (RA, calculated from root diameter measurements), root biomass (RB), total biomass (TB), and ratio between aerial and root biomass (A-RB). These independent variables were related to plant pull-out maximum resistance recorded during the removal ( $R_{\max}$ ), and time needed from the initiation of the pull-out to the maximum resistance value ( $T_{\text{to\_max}}$ ). Both  $R_{\max}$  and  $T_{\text{to\_max}}$  were obtained from the force-time curves of every individual.

As dependent data was not normally distributed, Generalised Linear Models were performed (GLM, multiple regression analysis, gamma distribution and log link function), including ‘species’ as grouping factor to evaluate whether the species affects significantly the relation between variables. Another GLM was used (separate-slope model) in order to evaluate whether the interaction between variables depends on the species. Finally, to determine the specific interaction of each species on the response variables, GLM per species (multiple regression) were conducted separately.

### 2.2.2. Evaluation of differences between species

The same variables mentioned before (RA, RB, TB, A-RB) were used to evaluate whether some species were more resistant to pull-out. In this case, the analysis was conducted considering only the mean value per species. In order to explore the role of root architecture on plant resistance to pull-out, the root of one specimen per species (randomly selected before the experiment) was scanned in order to have three additional independent variables: i.e. root length (RL), average root diameter (ARD), and root volume (RV).

All dependent variables followed a normal distribution, so the relation between dependent and independent variables was analysed using correlations and simple regressions. However, in order to be consistent with previous analyses, GLM were also performed (multiple regression, normal distribution, identity link function).

### 3. RESULTS

Each pull-out experiment produced a force vs. time curve, as those depicted in Fig. 3. Each curve starts from the same origin, and then the force-time curves tended to have a homogeneous slope in the rising limb. The maximum resistance ( $R_{\max}$ ) corresponds to the maximum force resisted by the roots before breaking. The time needed to reach the peak ( $T_{\text{to\_max}}$ ) was computed as the time interval from the first increment in resistance to the peak of the curve. The recession limb corresponds to the phase of the experiment when the roots (and in some cases a pan of soil) were extracted. As described in previous works (Bailey et al., 2002; Gregory, 2006; Edmaier et al., 2014), the recession limb in some cases registered small peaks that corresponded to small root breaking or loosening before the complete plant extraction.

#### 3.1. Pull-out resistance parameters

The maximum force needed to uproot the plants from their pots differed notably between species, in terms of both mean values and variability (Fig. 4a). *A. dealbata* is the species that showed less resistance to uprooting (mean = 22.64 N), while *E. illinita* was the species with higher resistance values (mean = 72.63 N). The range of values was also variable between species, being *M. boaria* and *E. illinita* those showing the larger variability ( $SD = \pm 32.70$  N and  $\pm 24.69$  N, respectively), and *L. caustica* the species with less variability ( $SD = \pm 7.65$  N). The minimum force value recorded was 2 N in an individual of *A. dealbata* while the maximum force (126 N) was measured in an individual of *E. illinita*. Variability in  $T_{\text{to\_max}}$  values was more homogeneous between species (Fig. 4b). The highest mean  $T_{\text{to\_max}}$  was observed in *M. boaria*, while the lowest in *Q. saponaria* (0.778 s and 0.411 s, respectively). Intraspecies variability was wide in all cases, being *C. alba* the species showing the lowest range of variability ( $SD = \pm 0.248$  s). The maximum value was measured in an individual of *A. chilensis* (i.e. 0.18 s), while the minimum (i.e. 0.1 s) was observed in individuals of all species except the *F. magellanica*.



### 3.2. Plant resistance to pull-out

Fig. 5 shows the maximum pull-out resistance values plotted against the selected plant predictor parameters.  $R_{\max}$  increased significantly with RA, RB and TB (Table 1). The A-RB ratio did not have a significant effect on  $R_{\max}$ , (not significant GLM p-values), which is also visible in the very scattered relationship between the two variables in Fig. 5c. The factor Species also significantly affected the response of a plant to a pull-out force (p-value <0.01). In turn,  $T_{\text{to\_max}}$  was significantly influenced by RA and TB (Table 1), but in this case the factor Species did not have an effect on it. Moreover, the interaction of Species and plant parameters had a clear influence on  $R_{\max}$ , but not on  $T_{\text{to\_max}}$  (Table 2).

### 3.3. Species effect on the resistance to pull-out

The mean  $R_{\max}$  was significantly correlated ( $p < 0.05$ ) to mean RB, mean TB, RV, and RL (Table 3). These relationships followed a positive linear regression with  $R^2 > 0.5$  in all four cases (Fig. 6). According to the linear regression analysis,  $T_{\text{to\_max}}$  was not significantly correlated to any of the plant parameters (Table 3). Fig. 6 shows that *E. illinita*, *A. chilensis* and *M. boaria* were the species with higher values in plant parameters and  $R_{\max}$ . Conversely, *A. dealbata* and *L. caustica* displayed in the bottom left part of the graphs, indicating that these were species with low values in plant parameters, and also low  $R_{\max}$  values.

### 3.4. Root architecture and plant pull-out

Root architecture was assessed both visually and considering the parameters obtained with WinRizho<sup>®</sup> scans before and after the growing period (see Table S2 in Supplementary material for results). *F. magellanica* was, by far, the species showing higher values of both root length and volume before the transplanting (i.e. 72.37 m and 8.68 cm<sup>3</sup>). After the growing period *A. chilensis*, *M. boaria*, and *E. illinita* were the species with longer roots (164.21 m, 133.74 m, and 113.93 m respectively), and higher root volumes (33.65 cm<sup>3</sup>, 26.29 cm<sup>3</sup>, and 36.48 cm<sup>3</sup>, respectively). The small growth of *F. magellanica* roots was probably due to some setbacks during the growing seasons. Indeed, *F. magellanica* experienced also the slower growth of the stem if compared with

all the other species (Table S2 in Supplementary material). Growth in RL and RV for *F. magellanica* individuals equalled 5.8% and 151.5%, respectively. Root increments in the other species were >300% in RL, and >500% in RV.

The 9 species used in the experiment were classified into 4 groups, according to the extent and geometry of their roots, based on visual observations and root scans data (Fig. 7). Group I included those species with a short thick principal root, several medium-sized roots, and a dense fine root network (i.e. *A. chilensis*, *E. illinita*, *F. magellanica*); Group II gathered the species with a long thick principal root, some medium-size roots, and a fine root network (i.e. *A. dealbata*, *L. caustica*, *Q. saponaria*); Group III included those species with a long thick principal root, few medium-size roots, and a semi-dense fine root network (i.e. *A. melanoxylon*, *M. boaria*); and finally, Group IV was composed of only one species (i.e. *C. alba*) which was characterised by a thick principal root and a dense fine-medium root network. This group configuration is consistent with the observed in the Fig. 8a (each colour represents a ‘morphology group’), where *A. chilensis* and *E. illinita* show high values and variability in the up-ramp SD curve, and *A. dealbata*, *L. caustica* and *Q. saponaria* show low slope values and less variability in the up-ramp SD. *F. magellanica* was not displayed in the upper part of the graph probably because this species had some growth setbacks, as stated above. The lower Fig. 8b plots the accumulated increment of plant resistance per accumulated increment of time. The curves with the highest slopes indicate that those species were extracted faster than the ones showing less slope.

## 4. DISCUSSION

### 4.1. Plants resistance to pull-out

#### 4.1.1. Plant parameters defining resistance to pull-out

The physical characteristics of the plants’ rooting systems are determinant for their resistance to uprooting. According to the results, the best descriptors for plant resistance to pull-out are RB, TB and RA. Further good parameters to infer pull-out resistance are RL and RV. The statistically significant relation between plant parameters and  $R_{\max}$  is positive in all cases, meaning that higher

values of RA, RB, TB, RV and RL lead to increased  $R_{\max}$ . Although this is the first quantification of this kind for riparian species in Chilean (and more generally south American) environments, this was somehow expected, as similar results were found in previous works (reported in the Introduction section; e.g. Hales et al., 2013; Edmaier et al., 2011, 2014; Bankhead et al., 2017; among others). The variable  $T_{\text{to\_max}}$  is particularly influenced by RA and TB, which may be related to the size or the weight of the plant.  $T_{\text{to\_max}}$  also depends on RL when considering mean values, probably related to the findings noted in previous analyses. Indeed, Edmaier et al. (2011) found that short roots were generally removed more easily than long roots. The species does not have an effect on  $T_{\text{to\_max}}$ , nor as a single factor nor in interaction with other species. This could be due to the relevant existing high intra-species variability, which is evident in the high dispersion of data and lack of trends. Given that only Edmaier et al. (2011) focused before on plant resistance to uprooting, comparison with previous evidence is not possible at this stage.

Although some of the previous works compared the resistance to pull-out of different species (e.g. Karrenberg et al., 2003; Bankhead et al., 2017), none of these assessed a wide range of species typical of riverine environments. The importance of the factor “Species” on the resistance to pull-out has been statistically demonstrated in this work, both when it is considered as a single factor and in interaction with the selected plant parameters. This suggests the existence of species-specific traits that are responsible for the differences between species as, for instance, root morphology, growth rate, and stem flexibility (e.g. Bornette et al., 2008; Kamchoom et al., 2014; Calvani et al., 2019, respectively). In fluvial environments, characterized by frequent and sudden floods in which plants are subject to high-energy events, the three factors are relevant for determining their resistance to uprooting.

#### *4.1.2. Root morphology and plant resistance to pull-out*

Among the species-specific traits that could affect the resistance to uprooting, in this paper we focused in root morphology. Despite the existing difficulties and challenges related to root characterisation (Stubbs et al., 2019), we visually classified the species used in the experiment in four groups according to their root morphology. Group I gathered species showing the highest

values of RB and TB, which were the parameters with the greater influence on pull-out variables (as shown by the GLM analyses). At the same time, these species also showed the highest  $R_{\max}$  values. *F. magellanica* showed lower values than *A. chilensis* and *E. illinita* probably because the water requirements of these species were higher than the average amount supplied during the growing period. Also, the upper parts of the roots of a few specimens of *F. magellanica* were partially affected by *Pseudococcus viburni* and ants that probably weakened the plant, causing at least 16 individuals plants to loose leaves (7 without any leaf and 9 with some leaves) and grow very slow. Group I roots were formed by a short thick principal root that divides into several (2 to 6) medium-sized roots. Probably, the medium-sized roots contributed to a high anchorage to the substrate since there were more attachment points. According to Mickovski et al. (2007), the presence and depth position of lateral roots have also an effect on the pull-out resistance, which could be reproduced by the root geometry described for the species in Group I. Kamchoom et al. (2014) also identified the heart-shaped roots (similar to roots of Group I) as the most resistant to pull-out. Groups II, III and IV were characterised by having one tap root that determines root anchorage force. Group III species had a higher density of fine-to-medium-sized roots than Group II, which would explain the greater resistance to pull-out of Group III species. Zhang et al. (2018) proved that the density of fine roots increased the soil shear strength, thus the resistance to be uprooted. Group IV (*Ca*) was the one with shallower roots. Although Kamchoom et al. (2014) identified plate-shaped roots (shallow roots, somehow similar to Group IV) as the less resistant, we found different results in this work. In this group, fine-medium roots were thicker than the fine network of the other groups, which could influence the measurements.

The relation curves between accumulated pull-out resistance until  $R_{\max}$  and the accumulated time until  $T_{\text{to\_max}}$  (Fig. 8b) were indicators of the promptness of the plant uprooting. Those specimens located in the right part of the graph registered slow velocities at the beginning of the pull-out, but increased with time. According to the results of this work, species belonging to Group III were representative for this extraction pattern, probably due to the high number of medium roots and the high density of fine roots that prevented a rapid uprooting. Conversely, those individuals

represented in the left part of the graph were extracted in a less variable (although not constant) velocity of uproot. Some species of Groups I and II were represented in this side of the graph.

#### 4.2. Interactions between flow strength and young riverine vegetation

Trying to relate the resistance to pull-out with the shear stress acting on a river bed that would be able to uproot the plants, we used an approach proposed by Calvani et al. (2019) for flexible juvenile seedlings. As in Eq. 4 of Calvani et al. (2019), we used the pull-out force ( $F_D$ , in N, as measured in our experiments in terms of  $R_{max}$ ) to determine the shear stress acting on the river bed ( $\tau_{bed}$ ) as:

$$F_D = \tau_{bed} \pi \left( H_p D_p + \frac{A_l}{\pi} + L_e \sum_{i=1}^{N_g} D_{r,i} \right) \quad \text{Eq. 1}$$

where  $D_p$  and  $H_p$  correspond to the diameter and height of the seedlings (in m) and were measured just before the pull-outs, and  $A_l$  corresponds to the foliage area (in  $m^2$ ), roughly estimated by multiplying the number of leaves by the area of a leaf (as the oval area calculation using length and width of an standard leaf). The area of the roots exposed by erosion ( $L_e$ ) that would be calculated based on the diameter ( $D_r$ ) and number of roots exposed ( $N_g$ ) was considered negligible in the first instance since no erosion occurred before the pull-outs. Estimations showed that, for the same  $R_{max}$ , the larger the  $A_l$ , the lower  $\tau_{bed}$  was needed to uproot the individual. This is due to the higher surface of plants in contact with water, which make it more susceptible to be pulled-out by the flow.

Taking into account a rectangular cross-section in an exemplary gravel-bed river with slope 1%, we also computed the flow shear stress ( $\tau$ , in  $N/m^2$ ) for different water stages corresponding to three different hydrological conditions: high flows, floods, and extraordinary floods (0.2 m, 1 m, and 3 m of water depth above the substrate, respectively). Once computed, we then associated the estimated  $\tau_{bed}$  values with the particle size movable at these water stages (i.e. 21.65 mm for the high flow, 108.23 mm for the flood, and 324.68 mm for the extraordinary flood). According to the calculations, the  $D_{50}$  used in the experiments (i.e. 15.67 mm) would be mobilised during a high flow pulse, while the maximum GSD class (i.e. it ranges between 31.5 and 45 mm) would move with

0.42 m of water depth above the substrate were plants were located. Regarding the individuals of the experiment, none of them would have been uprooted during high flows, and individuals of only some species (i.e. *A. dealbata*, *C. alba*, *F. magellanica*, *L. caustica*, *M. boaria*, and *Q. saponaria*) would be uprooted in a flood of 1 m water depth (see Supplementary Figure S1). An extraordinary flood would uproot individuals of all the species, being some of them completely removed (i.e. *C. alba*, *L. caustica*, and *Q. saponaria*).

According to this exercise, although a flood of 0.5 m of water depth would mobilise a large part of the substrate, the  $\tau$  in this case would be far below the  $\tau_{\text{bed}}$  values needed to uproot the individuals in the experiment due to a lower root anchorage (Type II erosion described by Edmaier et al., 2011). This finding indicates that erosion of the substrate would occur before the uprooting of these specimens. However, if the equation from Calvani et al. (2019) was to be applied considering bed erosion, the  $\tau_{\text{bed}}$  needed to uproot the specimen would be lower. Indeed, as the roots become exposed, there would be a larger portion of the plant area in contact with the flow (i.e. the exposed roots), and the strength of the roots would diminish because bed erosion would contribute to the loosening or detachment of the roots. In accordance to the results of the application of Eq. 4 from Calvani et al. (2019) and the findings of Edmaier et al. (2011), both elements would make the individuals more susceptible to be uprooted. Differences between species in the promptness of the uprooting could not be evaluated since no real measurements were done in individuals with exposed roots.

The most resistant species in the experiments do not coincide with the most resistant obtained when considering flow strength. While in the former case only the root resistance was measured, in the latter, the exercise incorporated both flow and the aerial part of the plant. These two elements changed the interpretation of the results. When considering water flow and aerial biomass, the exotic *A. dealbata* and *A. melanoxylon* were the most resisting species, likely due to the form and configuration of their leaves (although generally abundant, leaves are small and altogether occupy small areas). Although other intrinsic elements of the species could also affect the resistance to pull-out (e.g. stem flexibility, leaves stiffness), their aerial morphological configuration could be an

explanatory factor for the abundance of e.g. *A. dealbata* in fluvial environments. However, it was not possible to assess this fact in this experiment.

#### **4.3. Implications of vegetation growth and uprooting on river morpho-sedimentary dynamics**

The associated morphological changes in rivers related to vegetation presence have been widely assessed (e.g. Hupp and Rinaldi, 2007; Corenblit et al., 2007). For instance, some of the main responses to vegetation encroachment on river corridors are active channel narrowing and deepening, reduction of the number of active channels, and changes in flow hydraulics (e.g. Gran and Paola, 2001; Wang et al., 2015). Vegetation encroachment and growth stabilises river channel by root anchoring and preventing erosion from very early stages of development (e.g. Abernethy and Rutherford, 2001; Hubble et al., 2010). Vegetation prevents river bed from erosion by reducing flow velocity due to increased roughness, and also probably due to the carpet-like protection that the aerial part of the plants confer to the river bed when they bend (Termini, 2016).

The effect of vegetation on channel morphology depends on its type and density (Camporeale et al., 2013), but also on the hydrological regime of the fluvial system (Gurnell et al., 2012). Hence, magnitude and frequency of floods would finally determine the proportion of plants that detach and the proportion that remain attached to the river bed. In non-disturbed river systems, the presence of vegetation tends to be regulated by the hydrological regime (Corenblit et al., 2007). However, water management for agricultural, industrial and urban uses usually implies the reduction of flowing water or the modification of the discharge patterns. For instance, in semiarid areas or in regions where agriculture has an important role, reservoirs are basic to maintain the economic sustainability of the region. Below dams there is usually a lack of floods, and hence vegetation remains growing indefinitely. In these cases, and especially in those where exotic invasive vegetation is present, restoration actions may be useful to maintain fluvial dynamism and riparian habitat. For instance, dammed rivers may release controlled high water discharges (flushing flows) with sufficient energy to uproot very young specimens (Kui et al., 2014) located in river active bars (which should be submerged during the release). Similar actions have been performed before to remove excess vegetation encroachment on the river bed and proved to give good results (see the review of

Franklin et al., 2008). According to the results of our experiment, *A. dealbata* and *A. melanoxydon* specimens have low resistance to uprooting, but are not the ones firstly removed due to their aerial configuration, which could explain their high presence in river bars and margins. Despite being difficult to detach, and although during these actions it is not possible to discern between species, works should be performed in rivers where these species are present in order to prevent a wide spread out. The younger the seedlings, the better would probably be the results of preventive management actions, so they should be performed at a regular basis.

In the same sense, but in the opposite situation, e.g. need of bank stabilisation due to excess erosion, the most resisting plants used in this experiment could be used to reinforce these banks. Among the studied ones, *M. boaria* and *E. illinita* were the species resisting higher flow strengths, so they could be used in these restoration actions in Chilean environments. Also, given that the effectiveness in bank reinforcement actions is higher when multiple species are used for restoration (Allen et al., 2016), a combination of the studied species could be used.

#### **4.4. Representativity of the experiments**

The reproduction of fluvial environments in small facilities is often complex because it implies the scaling of both physical and ecological factors (Green, 2014). Also, scaling up the results from experiments is still a challenge for earth scientists (Rice et al., 2010). The experiments of this study reproduced substrate and vegetation interaction without the need of scaling none of the elements. In these experiments, the sediment mixture reproduced fairly well the grain size distribution of subsurface sediments in a gravel-bed river, ranging from pebbles to fine sand. Plants were also realistic in age and size for the context of the study, so the results obtained in the pull-out experiments can be considered representative for relatively active river bars with vegetation freshly sprout from seeds. In this case, although the experiments were not reproduced using water flow, the resistance opposed by the specimens was real and no correction was required to be compared to real conditions. Although in real floods vegetation tends to bend in the flow direction and the pulling angle is not vertical, previous experiments proved that the pulling angle does not substantially affect



the required force to uproot a plant (Gupta et al., 2008), so the results of this paper can be taken as representative for real environments.

## 5. CONCLUSIONS

The experiments carried out contribute to the knowledge of the interaction between ecology and fluvial geomorphology. The novelty of this study in comparison to other works using the same methodology is the number of species used in the analysis. This provides knowledge beyond the resistance to pull-out of different species, since the findings supply information for the design and implementation of management actions of riverine ecosystems. The results of these experiments show that despite the existing variability between individuals of the same species in terms of root characteristics (e.g. root biomass, root length, diameter), the factor species is important when studying plant resistance to erosion. When the analysis incorporates flow strength and the aerial part of the specimen instead of root parameters, results change and the species showing higher uprooting resistance vary. Given the importance of both factors: i) root morphology and dimensions (length, volume, diameter), and ii) the aerial part of the individual, some works could be focused on the construction of a model that combine these two elements. This would contribute to a more complete and better understanding of the predominant forces and prevailing mechanisms in submerged vegetation under flow stress.

The studied exotic invasive species did not show to be more resistant to uprooting than the native ones, so the wide spread of this species may probably be due to other causes. Moreover, and despite not having sufficient quantitative data to validate it, root morphology seems to be in some way related to the resistance to erosion of a plant. Among the studied roots, those similar to heart-shaped roots registered higher resistance values than those with a tap root. The effect of fine and medium-sized roots could be also assessed, and those roots with a high density of small roots tend to offer more resistance to pull-out. Further and longer experiments with a larger number of specimens of different ages would be interesting to assess the evolution of the species resistance to pull-out and to determine how the relation between root parameters (e.g. biomass, length, volume) and pull-out resistance behaves with time. Similar experiments could also investigate the bending resistance of

plants, which could recreate more realistic flow-vegetation interactions. Analogous pull-out experiments could be performed in real river bars in order to evaluate the behaviour of native and exotic plants, and which environmental (or location) factors influence the most the plant resistance to pull-out.

## ACKNOWLEDGEMENTS

This work was supported by the projects FONDECYT Postdoctorado 3180219, and FONDECYT Regular 1170657. We acknowledge Eduardo Arellano for ceding the WinRizho<sup>®</sup> software and equipment, and Juan Ovalle for his help with the scans. We also thank the Corporación Nacional Forestal of La Ligua for giving the individuals of *Acacia dealbata*.

## REFERENCES

- Abernethy, B., Rutherford, I.D. (2001). The distribution and strength of riparian tree roots in relation to riverbank reinforcement. *Hydrological Processes*, 15: 63-79. DOI: 10.1002/hyp.152
- Allen, D.C., Cardinale, B.J., Wynn-Thompson, T. (2016). Plant biodiversity effects in reducing fluvial erosion are limited to low species richness. *Ecology*, 97 (1): 17-24. DOI: 10.1890/15-0800.1
- Arianoutsou, M., Delipetrou, P., Celesti-Grapow, L., Basnou, C., Bazos, I., Kokkoris, Y., Blasi, C., Vilà, M. (2010). Comparing naturalized alien plants and recipient habitats across an east-west gradient in the Mediterranean Basin. *Journal of Biogeography*, 37: 1811-1823. DOI: 10.1111/j.1365-2699.2010.02324.x
- Bailey P.H.J., Currey, J.D., Fitter, A.H. (2002). The role of root system architecture and root hairs in promoting anchorage against uprooting forces in *Allium cepa* and root mutants of *Arabidopsis thaliana*. *Journal of Experimental Botany*, 53 (367): 333-340. DOI: 10.1093/jexbot/53.367.333
- Bankhead, N.L., Thomas, R. E., Simon, A. (2017). A combined field, laboratory and numerical study of the forces applied to, and the potential for removal of, bar top vegetation in a braided river. *Earth Surface Processes and Landforms*, 42: 439-459. DOI: 10.1002/esp.3997

466 Batalla, R.J., Iroumé, A., Hernández, M., Llena, M., Mazzorana, B., Vericat, D. (2018). Recent  
 467 geomorphological evolution of a natural river channel in a Mediterranean Chilean basin.  
 468 *Geomorphology*, 303: 322-337. DOI: 10.1016/j.geomorph.2017.12.006

469 Bornette, G., Tabacchi, E., Hupp, C., Puijalon, S., Rostan, J.C. (2008). A model of plant strategies  
 470 in fluvial hydrosystems. *Freshwater biology*: 53: 1692-1705. DOI: 10.1111/j.1365-  
 471 2427.2008.01994.x

472 Bywater-Reyes, S., Wilcox, A.C., Stella J.C., Lightbody, A.F. (2015). Flow and scour constraints  
 473 on uprooting of pioneer woody seedlings. *Water Resources Research*, 51: 9190-9206. DOI:  
 474 10.1002/2014WR016641

475 Calvani, G., Francalanci, S., Solari, L. (2019). A Physiscal Model for the Uprooting of Flexible  
 476 Vegetation on River Bars. *Journal of Geophysical Research: Earth Surface*, 124: 1018-1034. DOI:  
 477 10.1029/2018JF004747

478 Camporeale, C., Perucca, E., Ridolfi, L., Gurnell, A.M. (2013). Modeling the interactions between  
 479 river morphodynamics and riparian vegetation. *Reviews of Geophysics*, 51: 2012RG000407. DOI:  
 480 10.1002/rog.20014

481 Capilleri, P.P., Motta, E., Raciti, E. (2016). Experimental study on native plant root tensile strength  
 482 for slope stabilization. *Procedia Engineering*, 158: 116-121. DOI: 10.1016/j.proeng.2016.08.415

483 Castro-Díez, P., Alonso, A. (2017). Effects of non-native riparian plants in riparian and fluvial  
 484 ecosystems: a review for the Iberian Peninsula. *Limnetica*, 36 (2): 525-541. DOI:  
 485 10.23818/limn.36.19

486 Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M. (2007). Reciprocal interactions and  
 487 adjustment between fluvial landforms and vegetation dynamics in river corridors: a review of  
 488 complementary approaches. *Earth-Science Reviews*. 84: 56-86. DOI:  
 489 10.1016/j.earscirev.2007.05.004

490 Crouzy, B., Edmaier, K., Pasquale, N., Perona, P. (2013). Impact of floods on the statistical  
491 distribution of riverbed vegetation. *Geomorphology*, 202: 51-58. DOI:  
492 10.1016/j.geomorph.2012.09.013

493 Crouzy, B., Edmaier, K., Perona, P. (2014). Biomechanics of plant anchorage at early development  
494 stage. *Journal of Theoretical Biology*, 363: 22-29. DOI: 10.1016/j.jtbi.2014.07.034

495 Čuda, J., Rumlerová, Z., Bruna, J., Skálová, H., Pyšek, P. (2017). Floods affect the abundance of  
496 invasive *Impatiens glandulifera* and its spread from river corridors. *Diversity and Distributions*, 1-  
497 13. DOI: 10.1111/ddi.12524

498 Edmaier, K., Burlando, P., Perona, P. (2011). Mechanisms of vegetation uprooting by flow in  
499 alluvial non-cohesive sediment. *Hydrological Earth Systems Sciences*, 15: 1615-1627. DOI:  
500 10.5194/hess-15-1615-2011

501 Edmaier, K., Crouzy, B., Ennos, R., Burlando, P., Perona, P. (2014). Influence of root  
502 characteristics and soil variables on the uprooting mechanics of *Avena Sativa* and *Medicago sativa*  
503 seedlings. *Earth Surface Processes and Landforms*, 39: 1354-1364. DOI: 10.1002/esp.3587

504 Edmaier, K., Crouzy, B., Perona, P. (2015). Experimental characterization of vegetation uprooting  
505 by flow. *Journal of Geophysical Research*, 120: 1812-1824. DOI: 10.1002/2014JG002898

506 Franklin, P., Dunbar, M., Whitehead, P. (2008). Flow controls on lowland river macrophytes: A  
507 review. *Science of the Total Environment*, 400: 369-378. DOI: 10.1016/j.scitotenv.2008.06.018

508 Fuentes-Ramírez, A., Pauchard, A., Marticorena, A., Sánchez, P. (2010). Relación entre la invasión  
509 de *Acacia dealbata* Link (Fabaceae: Mimosoideae) y la riqueza de especies vegetales en el centro-  
510 sur de Chile. *Gayana Botanica*, 67 (2): 188-197. DOI: 10.4067/S0717-66432010000200004

511 Fuentes, N., Sánchez, P., Pauchard, A., Urrutia, J., Cavieres, L., Marticorena, A. (2014). Plantas  
512 invasoras del centro-sur de Chile: Una guía de campo. Laboratorio de Invasiones Biológicas (LIB),  
513 Concepción, Chile.

514 Giadrossich, F., Schwarz, M., Cohen, D., Cislighi, A., Vergani, C., Hubble, T., Phillips, C., Stokes,  
 515 A. (2017). Methods to measure the mechanical behaviour of tree roots: A review. *Ecological*  
 516 *Engineering*, 109: 256-271. DOI: 10.1016/j.ecoleng.2017.08.032

517 Gran, K., Paola, C. (2001). Riparian vegetation control on braided stream dynamics. *Water*  
 518 *Resources Research*, 37 (12): 3275-3283. DOI: 10.1029/2000WR000203

519 Green, D.L. (2014). *Modelling Geomorphic Systems: Scaled Physical Models*. *Geomorphological*  
 520 *Techniques*, Chap. 5, Sec 3.

521 Gregory, P. (2006). *Plant Roots. Growth, Activity and Interaction with Soils*. Smith A. (ed).  
 522 Blackwell: Oxford, UK.

523 Gupta, R.A., Singh, S., Sharda, V. (2008). Study on Pull Force for Cotton Stalk and its Relation  
 524 with Crop and Soil Parameters. *Journal of the Institution of Engineers (India): Agricultural*  
 525 *Engineering Division*.

526 Gurnell, A.M., Bertoldi, W., Corenblit, D. (2012). Changing river channels: The role of  
 527 hydrological processes, plants and pioneer fluvial landforms in humid temperate, mixed load, gravel  
 528 bed rivers. *Earth-Science Reviews*, 111: 129-141. DOI: 10.1016/j.earscirev.2011.11.005

529 Gurnell, A. (2014). Plants as river system engineers. *Earth Surface Processes and Landforms*, 39: 4-  
 530 25. DOI: 10.1002/esp.3397

531 Hales, T.C., Cole-Hawthorne, C., Lovell, L., Evans, S.L. (2013). Assessing the accuracy of simple  
 532 field based root strength measurements. *Plant Soil*, 372: 553-565. DOI: 10.1007/s11104-013-1765-2

533 Hood, W.G., Naiman, R.J. (2000). Vulnerability of riparian zones to invasion by exotic vascular  
 534 plants. *Plant Ecology*, 148: 105-114. DOI: 10.1023/A:1009800327334

535 Hubble, T.C.T., Docker, B.B., Rutherford, I.D. (2010). The role of riparian trees in maintaining  
 536 riverbank stability: A review of Australian experience and practice. *Ecological Engineering*, 36:  
 537 292-304. DOI: 10.1016/j.ecoleng.2009.04.006

538 Hupp, C.R., Rinaldi, M. (2007). Riparian Vegetation Patters in Relation to Fluvial Landforms and  
 539 Channel Evolution along Selected Rivers of Tuscany (Central Italy). *Annals of the Association of*  
 540 *American Geographers*, 97 (1): 12-30. DOI: 10.1111/j.1467-8306.2007.00521.x

541 Kamchoom, V., Leung, A.K., Ng, C.W.W. (2014). Effects of root geometry and transpiration on  
 542 pull-out resistance. *Géotechnique Letters*, 4: 330-336. DOI: 10.1680/geolett.14.00086

543 Karrenberg, S., Blaser, S., Kollmann, J., Speck, T., Edwards, P.J. (2003). Root anchorage of  
 544 samplings and cuttings of woody pioneer species in a riparian environment. *Functional Ecology*, 17:  
 545 170-177. DOI: 10.1046/j.1365-2435.2003.00709.x

546 Kui, L., Stella, J.C., Lightbody, A., Wilcox, A.C. (2014). Ecogeomorphic feedbacks and flood loss  
 547 of riparian tree seedlings in meandering channel experiments. *Water Resources Research*, 50: 9366-  
 548 9384. DOI: 10.1002/2014WR015719

549 Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.J., Holmes, P.M., Pauchard, A., O'Farrell,  
 550 P.J., Rogers, A.M., Blanchard, R., Blignaut, J., Richardson, D.M. (2011). Impacts of invasive  
 551 Australian acacias: Implications for management and restoration. *Diversity & Distributions*, 17(5):  
 552 1015–1029. DOI: 10.1111/j.1472-4642.2011.00816.x

553 Mickovski, S.B., Bengough, A.G., Bransby, M.F., Davies, M.C.R., Hallet, P.D., Sonnenberg, R.  
 554 (2007). Materials stiffness, branching pattern and soil matric potential affect the pullout resistance  
 555 of model root systems. *European Journal of Soil Science*, 58: 1471-1481. DOI: 10.1111/j.1365-  
 556 2389.2007.00953.x

557 Osman, N., Abdullah, M.N., Abdullah, C.H. (2011). Pull-Out and Tensile Strength Properties of  
 558 Two Selected Tropical Trees. *Sains Malaysiana*, 40(6): 577-585.

559 Perona, P., Molnar, P., Crouzy, B., Perucca, E., Jiang, Z., McLelland, S., Wüthrich, D., Edmaier,  
 560 K., Francis, R., Camporeale, C., Gurnell, A. (2012). Biomass selection by floods and related

561 timescales: Part 1. Experimental observations. *Advances in Water Resources*, 39: 85-96. DOI:  
562 10.1016/j.advwatres.2011.09.016

563 Pollen, N. (2007). Temporal and spatial variability in root reinforcement of streambanks:  
564 Accounting for soil shear strength and soil moisture. *Catena*, 69: 197-205. DOI:  
565 10.1016/j.catena.2006.05.004

566 Pyšek, P., Prach, K. (1994). How Important are Rivers for Supporting Plant Invasions? In: de Waal,  
567 L.C., Child, L.E., Wade, P.M., Brock, J.H. (Eds). *Ecology and Management of Invasive Riverside*  
568 *Plants*. Wiley, Chichester.

569 Richardson, D.M., Holmes, P.M. Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P.,  
570 Pyšek, P., Hobbs, R.J. (2007). Riparian vegetation: degradation, alien plant invasions, and  
571 restoration prospects. *Diversity and Distributions*, 13: 126-139. DOI: 10.1111/j.1472-  
572 4642.2006.00314.x

573 Rice, S., Lancaster, J., Kemp, P. (2010). Experimentation at the interface of fluvial geomorphology,  
574 stream ecology and hydraulic engineering and the development of an effective interdisciplinary  
575 river science. *Earth Surface Processes and Landforms*, 35: 64-77. DOI: 10.1002/esp.1838

576 Stubbs, C.J., Cook, D.D., Niklas, K.J. (2019). A general review of the biomechanics of root  
577 anchorage. *Journal of Experimental Botany*, 70 (14): 3439–3451. DOI: 10.1093/jxb/ery451

578 Termini, D. (2016). Reduction of scouring downstream of a rigid bed by means of a vegetated  
579 carpet: experimental investigation in a laboratory flume. *Environmental Fluid*  
580 *Mechanics*, 16, 1111–1127. DOI: 10.1007/s10652-016-9467-y

581 Wang, G., Mang, S., Cai, H., Liu, S., Zhang, Z., Wang, L., Innes, J.I. (2015). Integrated watershed  
582 management: evolution, development and emerging trends. *Journal of Forestry Research*, 27 (5):  
583 967-994. DOI: 10.1007/s11676-016-0293-3

584 Xavier, P., Wilson, C., Aberle, J., Rauch, H.P., Schoneboom, T., Lammeranner, W., Thomas, H.  
585 (2010). Drag force of flexible submerged trees. Proceedings of the HYDRALAB III Joint User  
586 Meeting, Hannover, Germany. 278 pp.

587 Zhang, D., Cheng, J., Liu, Y., Zhang, H., Ma, L., Mei, X., Sun, Y. (2018). Spatio-Temporal  
588 Dynamic Architecture of Living Brush Mattress: Root System and Soil Shear Strength in  
589 Riverbanks. *Forests*, 9: 943. DOI: DOI: 10.3390/f9080493

590



## FIGURE CAPTIONS

**Fig 1.** Grain size distribution of the sediments used in the experiments. Fine sediments ( $< 2$  mm) are included in one single class.

**Fig 2.** a) General view of the plant nursery days before the plant pull-out experiments; b) View of the plant before de pull-out; c) Plant pulling mechanism: tripod, electric winch and cell load; d) Detailed view of the carabiner attached to the stem; e) View of roots after the pull-out.

**Fig 3.** Examples of force-time curves of five individuals used in the experiment. Note that they are individual examples and that they cannot be taken as representative for each species. Inset graph shows graphically some of the concepts used along the article.

**Fig 4.** Maximum resistance (a) and pulling-out duration to reach max resistance (b) per species. For each case, the mean (black dot), the standard errors (box), and the standard deviation (whiskers) are shown.

**Fig 5.** Relation between plant parameters a) Root area, b) Root biomass, c) Aerial/root biomass, and d) Total biomass and maximum resistance measured for each individual. Note that data is treated all together and not separated per species ( $n = 180$ ).

**Figure 6.** Mean maximum resistance as a function of selected plant parameters per species ( $n = 9$ , one per species). Only statistically significant relations ( $p < 0.05$ ) are shown.

**Figure 7.** Roots of four individuals at the end of the growing period. a) *Lithraea caustica* (Group II); b) *Cryptocarya alba* (Group IV); *Maytenus boaria* (Group III); and d) *Fuchsia magellanica* (Group I).

**Figure 8.** a) Box plot for the standard deviation of the up-ramp pull-out curves per species. b) Example curves for the relative accumulated resistance to pull-out for the up-ramp curve vs. relative accumulated time per species.

**Table 1.** GLM analysis to assess the influence of the selected plant parameters to pull-out resistance variables. Significant values are marked in bold (level of significance established at  $p \leq 0.05$ ).

	Max resistance		Time to max	
	Chi- Square	p-value	Chi- Square	p-value
Root area	<b>23.41</b>	<b>&lt;0.01</b>	<b>5.23</b>	<b>0.02</b>
Root biomass	<b>53.58</b>	<b>&lt;0.01</b>	1.51	0.22
Total biomass	<b>26.38</b>	<b>&lt;0.01</b>	<b>4.99</b>	<b>0.03</b>
Aerial/root biomass	1.10	0.29	0.13	0.71
Species	<b>46.25</b>	<b>&lt;0.01</b>	12.45	0.13

**Table 2.** GLM analysis to assess the interaction between the species (factor) and plant parameters (continuous predictors), as well as their influence on the pull-out variables. Significant values are marked in bold (level of significance established at  $p \leq 0.05$ ).

	Max resistance		Time to max	
	Chi- Square	p-value	Chi- Square	p-value
Species × Root area	<b>92.35</b>	<b>&lt;0.01</b>	15.26	0.08
Species × Root biomass	<b>36.00</b>	<b>&lt;0.01</b>	9.51	0.39
Species × Total biomass	<b>25.13</b>	<b>&lt;0.01</b>	7.15	0.62
Species × Aerial/root biomass	<b>20.49</b>	<b>0.02</b>	16.18	0.06
Species	14.50	0.07	13.43	0.10

**Table 3.** Relation between plant descriptor parameters and pull-out variables (n = 9, one per species). Significant values are marked in bold (level of significance established at  $p \leq 0.05$ ).).

	Max resistance			Time to max		
	GLM analysis		Linear regression analysis		Linear regression analysis	
	Chi-Square	p-value	R <sup>2</sup>	p-value	Chi-Square	p-value
Mean root area	2.40	0.12	0.23	0.19	2.61	0.11
Mean root biomass	<b>7.93</b>	<b>0.00</b>	<b>0.64</b>	<b>0.01</b>	1.09	0.30
Total biomass	<b>5.42</b>	<b>0.02</b>	<b>0.74</b>	<b>0.00</b>	1.69	0.19
Aerial/root biomass	1.50	0.22	0.04	0.59	1.03	0.31
Root volume	0.10	0.76	<b>0.70</b>	<b>0.01</b>	1.38	0.24
Average diameter	0.43	0.51	0.02	0.72	1.91	0.17
Root length	2.84	0.09	<b>0.51</b>	<b>0.03</b>	<b>8.39</b>	<b>0.00</b>

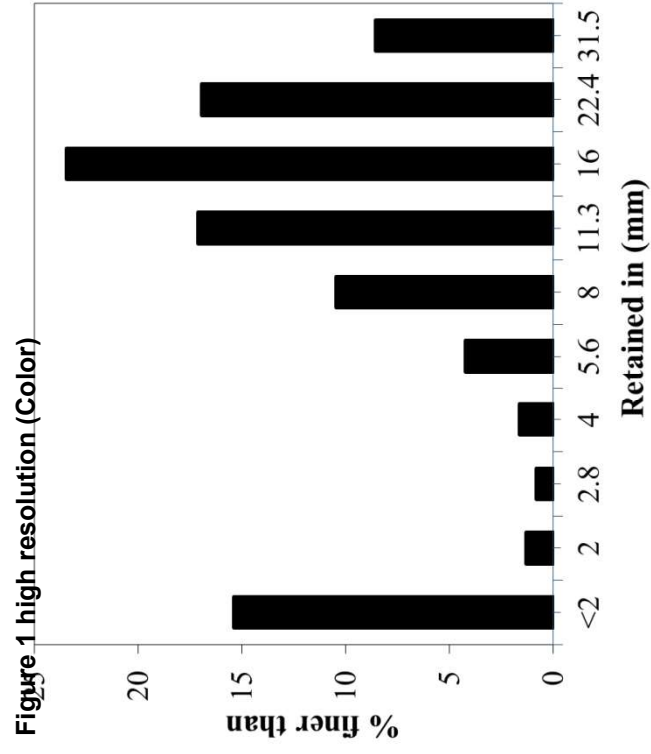


Figure 2 high resolution (Color)



Figure 3 high resolution (Color)

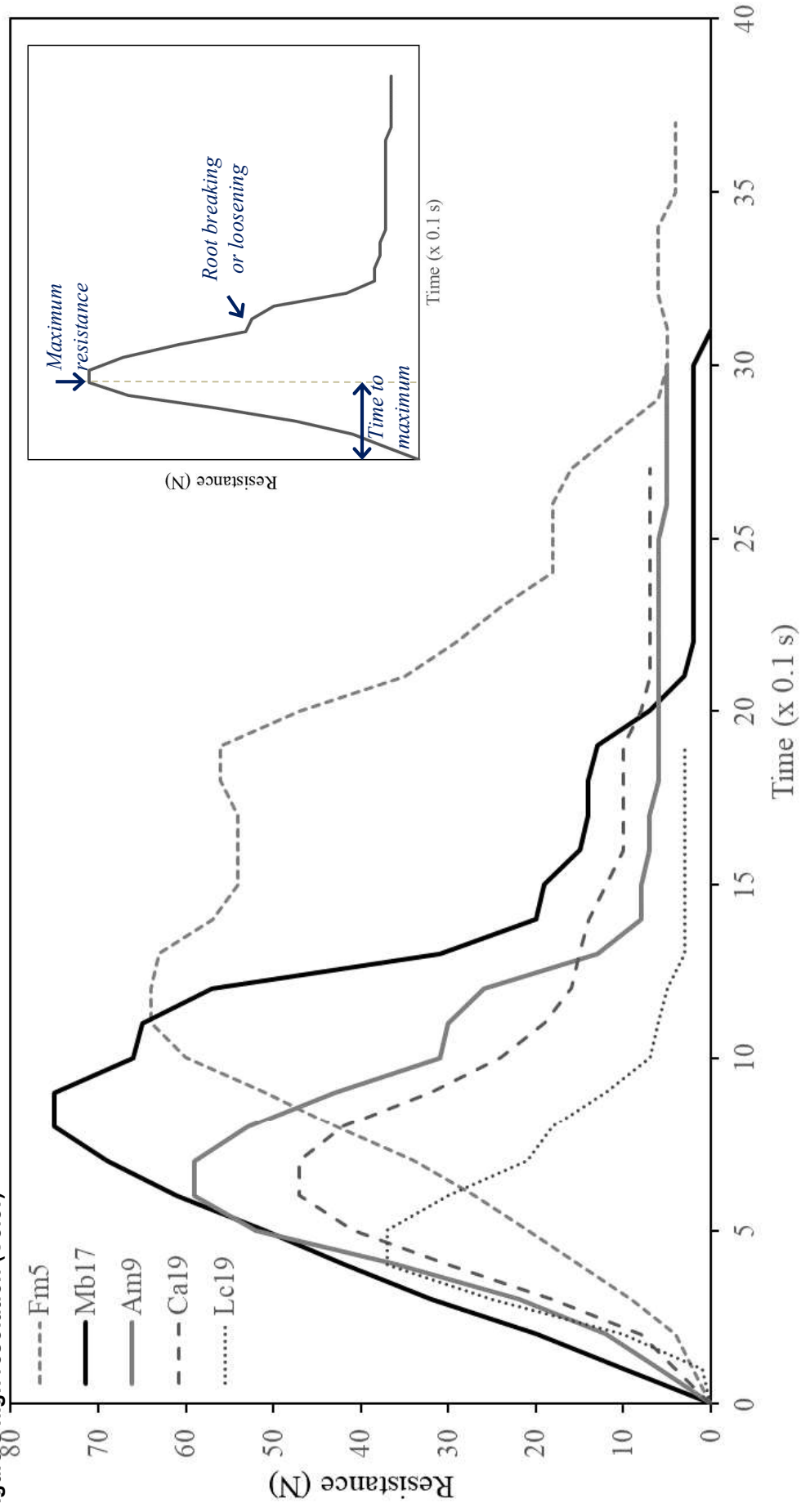
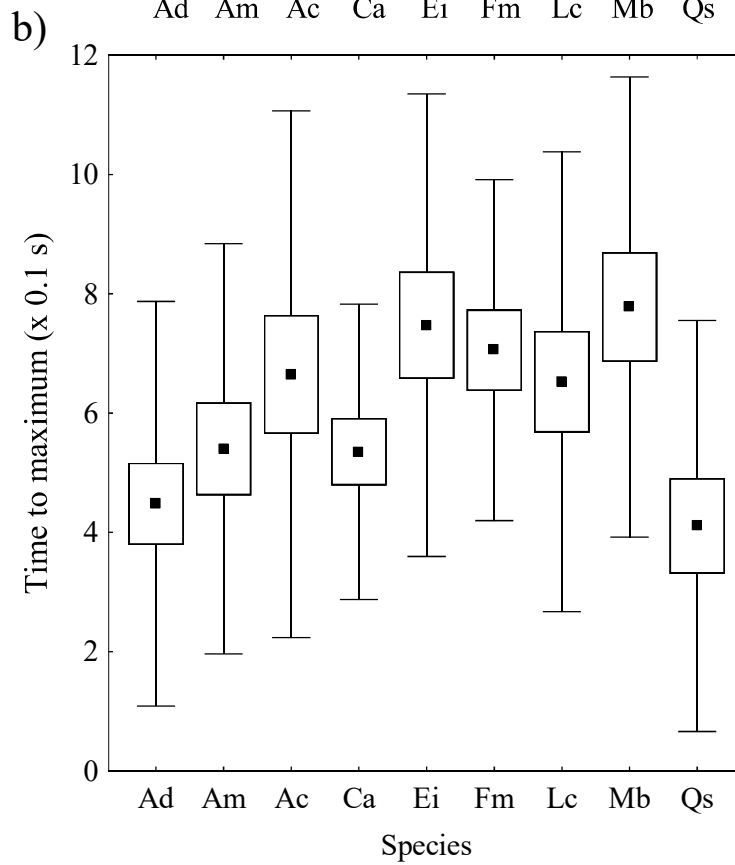
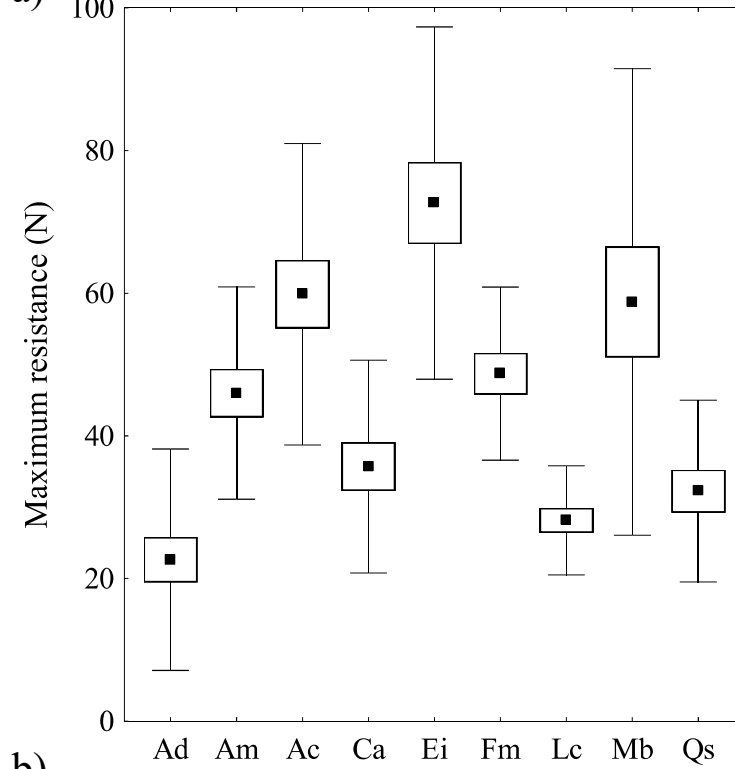
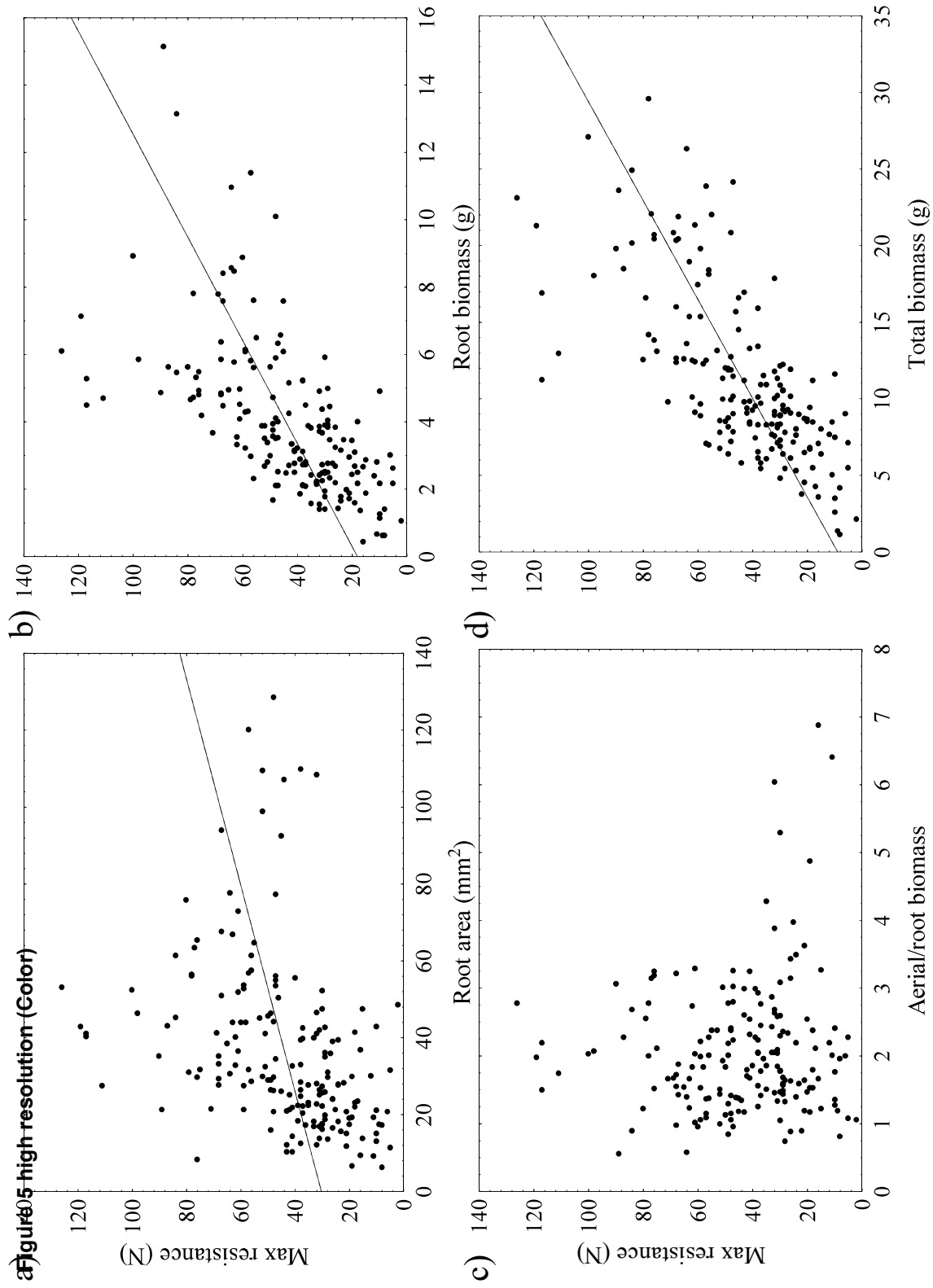


Figure 4 high resolution (Color)







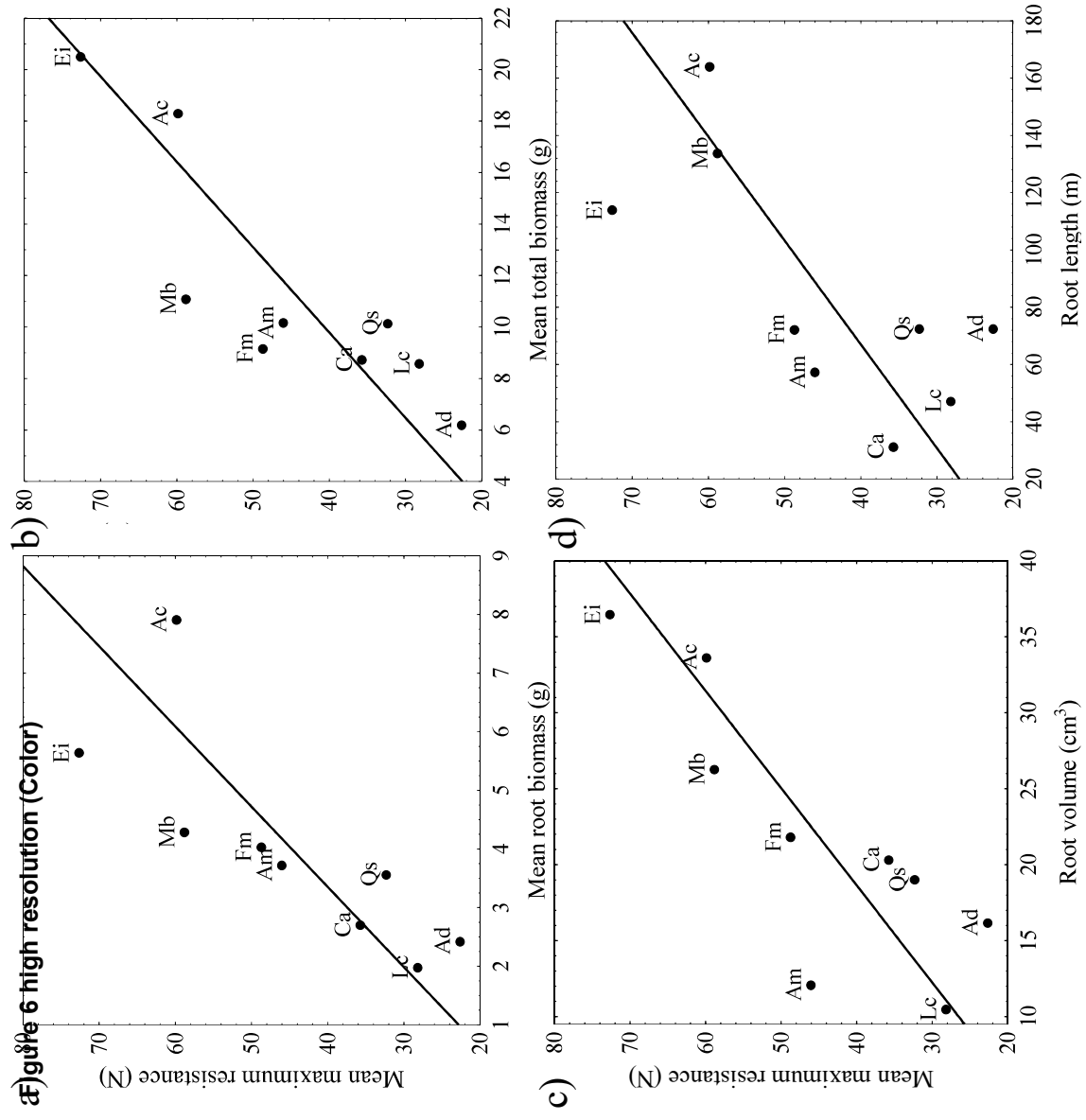
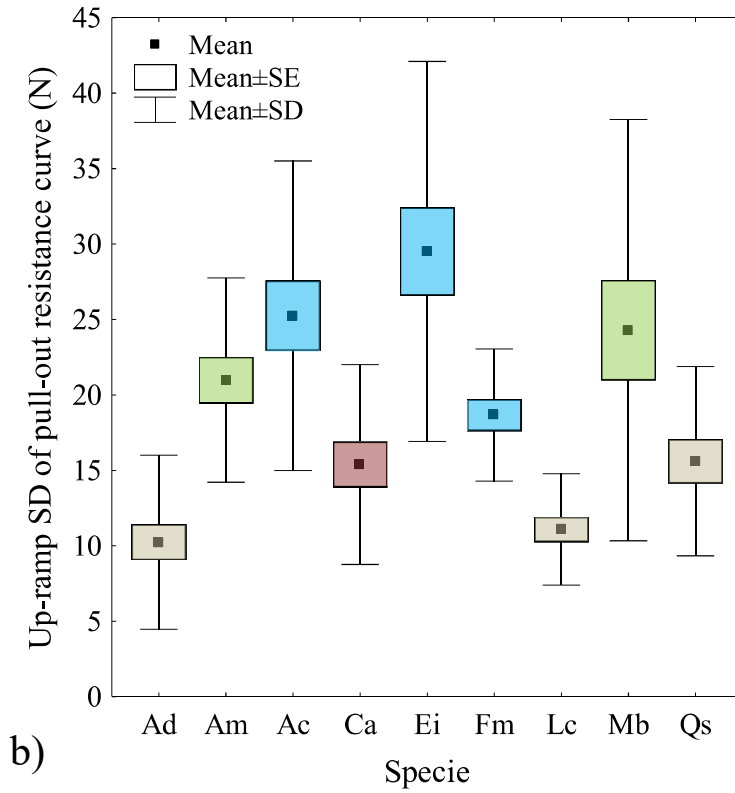


Figure 7 high resolution (Color)



**Figure 8 high resolution (Color)**



b)

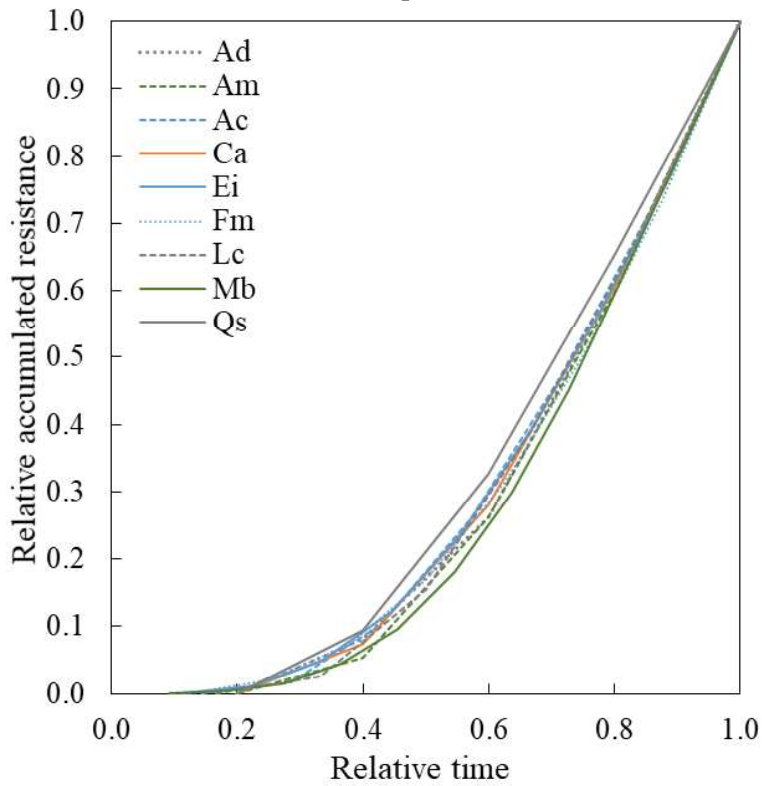


Figure 2 high resolution (Greyscale)

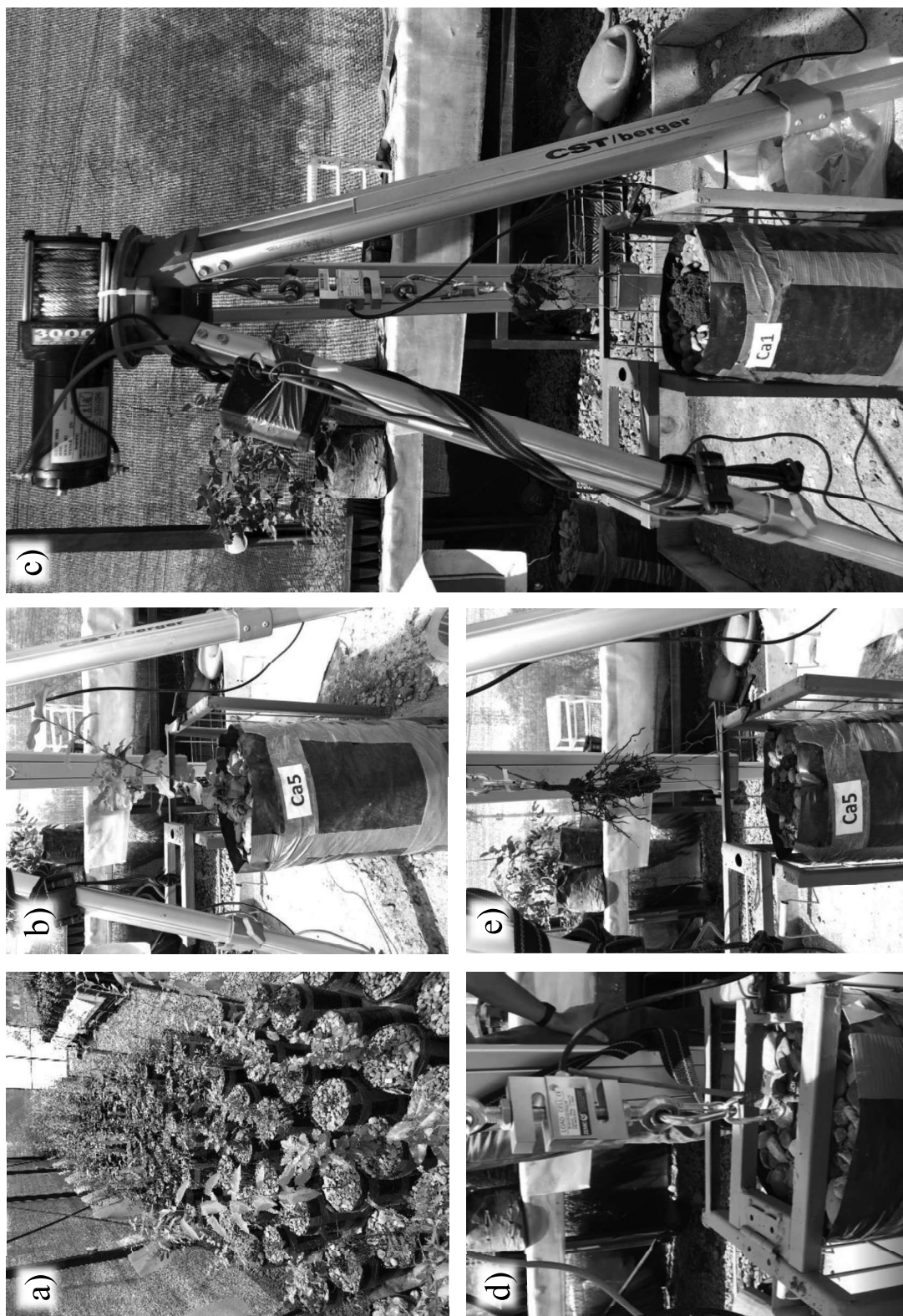


Figure 7 high resolution (Greyscale)

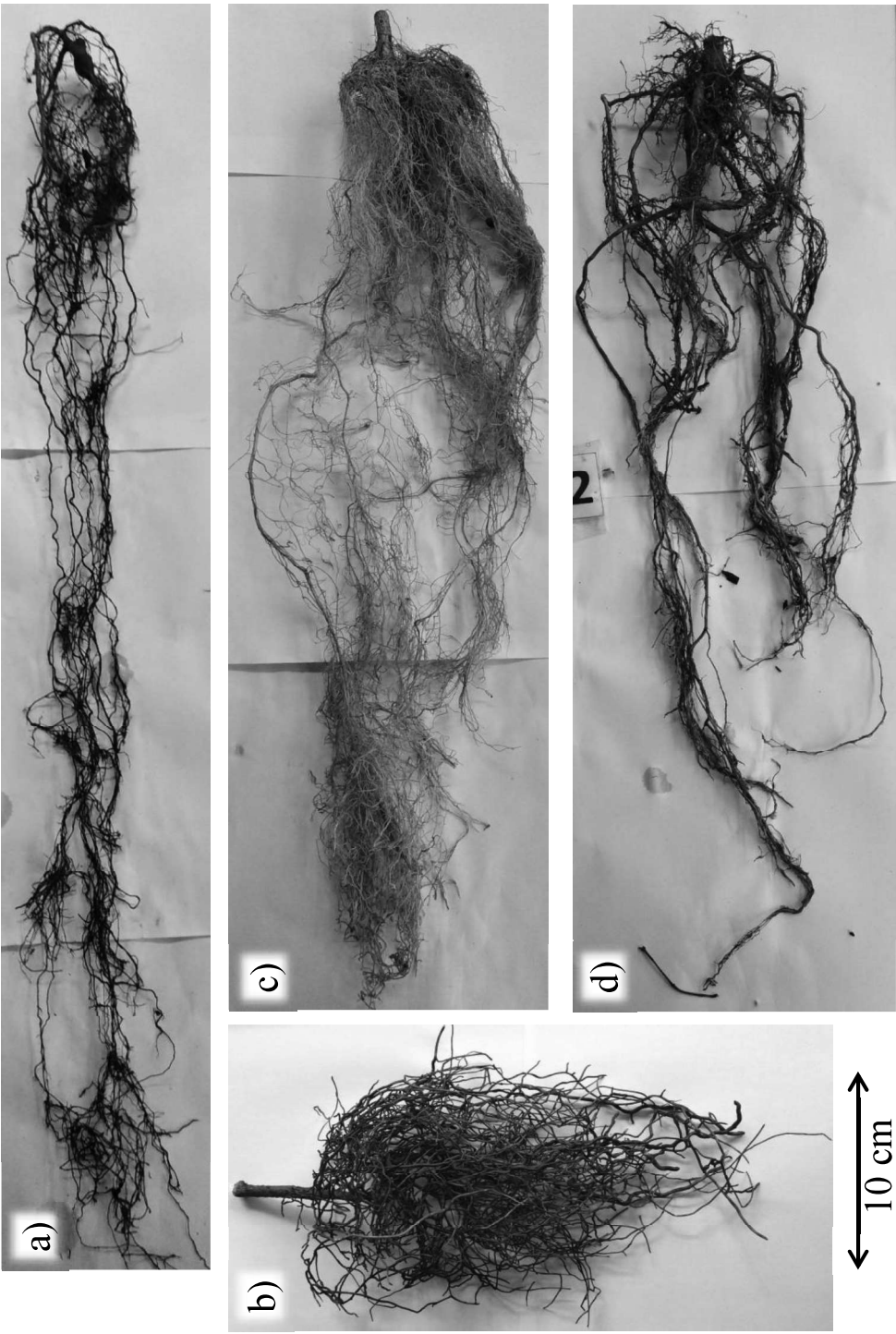


Figure 8 high resolution (Greyscale)

